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Multitrophic interactions in space: metacommunity dynamics in fragmented landscapes

Introduction

The distribution and abundance of consumers are necessarily limited by the distribution and abundance of their resources. With the exception of obligate mutualisms, a species at a higher trophic level in a food chain will occupy a subset of the locations occupied by species at lower trophic levels (Holt, 1995, 1997). In order to persist, species at higher trophic levels must be able to colonize, at a sufficiently high rate, sites occupied by populations of the lower trophic level species. The interaction may be spatially dynamic in both directions because species at any trophic level may influence the dynamics of one another. Once the interacting species occur as local populations in a shared habitat patch, phenomena traditionally addressed by studies of multitrophic interaction take place. Thus for species living in fragmented landscapes it is critical to keep in mind both processes occurring at large spatial scales and those occurring within a single habitat patch or local population. This chapter is about the interplay between spatial dynamics and multitrophic level interactions.

Species involved in a trophic interaction, such as the interaction between a predator and its prey, are influenced directly and indirectly by the trophic levels above and below them. The indirect effect of a non-adjacent trophic level can be either positive or negative. For example, herbivorous hosts may be concealed from (Weis and Abrahamson, 1985; Hawkins et al., 1990) or exposed to (Price et al., 1980; Walde, 1995a; Turlings et al., 1995, chapter 7, this volume; Thaler, 1999) a foraging parasitoid by attributes of their food plant. Similarly, attributes of a herbivore and/or its food plant may protect a parasitoid from hyperparasitism (Weis and Abrahamson, 1985; Yeargan and Braman, 1989) or alternatively,

increase susceptibility of a parasitoid to hyperparasitism (Singh and Srivastava, 1988; van Baarlen et al., 1996; Sullivan and Völk, 1999). Within communities, the indirect effects of the lower and upper trophic levels can either increase or decrease the stability of populations, by moderating the use of a potentially limiting resource or by facilitating the consumption of the resource until it has gone locally extinct.

The primary focus of the study of multitrophic interactions is to analyze and comprehend the attributes of organisms that influence non-adjacent trophic levels either directly or indirectly. One such attribute of an organism is its spatial distribution (dispersion), both within and among habitat patches suitable for occupancy. Distribution is generally viewed as the outcome of many ecological processes, and is influenced by the many ecological factors traditionally labeled as habitat requirements and niche. We can also consider distribution as another attribute of an organism, which potentially affects its trophic interactions as much as, or even more than its chemical makeup, sensory perception, phenology, growth rate, and other such factors. The addition of the spatial structure of the landscape and spatial population dynamics to the study of multitrophic interactions is becoming an increasingly necessary consideration with increasing fragmentation of many natural environments.

Expansion of the study of multitrophic interactions to include space introduces two complementary ecological phenomena. First is the extent to which trophic interactions among individuals taking place at the scale of local populations (e.g. foraging behavior, prey preference, and density-dependent behaviors) might affect the dynamics at the regional or meta-population scale. Second is how large-scale population dynamics, such as migration among populations and extinction–colonization dynamics, might affect local multitrophic interactions.

In the following section, we briefly outline the theory of multitrophic interactions in fragmented landscapes, which is essentially the theory of metapopulation dynamics (for a review see Hanski, 1999) extended to several interacting species. We then discuss selected empirical findings from the literature that illustrate the range of questions asked by ecologists. The rest of this chapter is devoted to a more detailed analysis of multitrophic interactions in a community of two host plant species, one herbivorous insect, two primary parasitoids and two hyperparasitoids, which occurs in a highly fragmented landscape and which we and others have studied over the past several years as an example of a small metacommunity.

Brief overview of theory

A metapopulation is an assemblage of locally breeding conspecific populations that are connected via migration (Hanski and Gilpin, 1997). The viability of a classical metapopulation, with no extinction-resistant "mainland" populations (Harrison, 1991), depends on the rates of local extinction and colonization, and on the degree of asynchrony in local population dynamics (Hanski, 1998). Interacting species, each with their own spatial population structure, may persist as single populations, patchy populations, or as metapopulations (Harrison and Taylor, 1997) in the same fragmented landscape, primarily depending on the scale of migration and hence the degree of mixing of neighboring populations. For example, a single patchy plant population might support a herbivore metapopulation, which might support a relatively continuous parasitoid population (a mobile species), which in turn might support a hyperparasitoid metapopulation (a more sedentary species). The stability of the entire system would clearly depend on the spatial population structures of each species (Taylor, 1988, 1991).

The natural theoretical framework to consider the spatial dimension of multitrophic interactions is to expand single-species metapopulation models to several interacting species. Robert Holt (1995, 1997) in particular has developed such a theory with simple patch occupancy models, extending the previously studied two-species competition (Levins and Culver, 1971; Slatkin, 1974; Hanski, 1983, 1999; Nee and May, 1992; Nee *et al.*, 1997) and predator–prey models (Taylor, 1991; May, 1994; Harrison and Taylor, 1997; Nee *et al.*, 1997; Hassell, 2000) to three or more species. The key assumptions made by Holt (1997) are that the food chain in a particular habitat patch is built up via sequential colonization, and that the extinction of a prey population automatically leads to the extinction of the predator population (and, naturally, any species at even higher trophic levels). The most noteworthy simplification of the models is the presence–absence description of local populations, common to all patch occupancy models (Hanski, 1999). Structured models, involving a description of local dynamics as well as of metapopulation dynamics, have been constructed and analyzed for two species at most (e.g., Reeve, 1988; Hassell *et al.*, 1991; Rohani *et al.*, 1996).

A basic conclusion emerging from the models is that metapopulation dynamics can constrain the length of specialist food chains in fragmented landscapes, that is, species located at higher trophic levels may not be able

to persist in a landscape where the species at lower trophic levels are specialized to an uncommon habitat or have a restricted distribution for other reasons. In certain situations, alternative stable states may occur, such that an intermediate predator can only occur in the presence of the top predator (Holt, 1997).

In heterogeneous fragmented landscapes, with more than one kind of habitat patch present, species may persist either by being specialists on one patch type with low extinction and/or high colonization rate, or by being generalists and thereby having access to a larger number of habitat patches, which by itself facilitates colonization. Different species in a multitrophic interaction may exhibit different degrees of specialization. For instance, a predator may use two alternative prey species each specializing in a different habitat type, and thereby the predator population generates an indirect interaction between the prey species in a mosaic of the two types of habitat (Holt, 1997). It is clear that the complexities that one may build up with such considerations for multitrophic interactions are considerable – not only do we have a web of interspecific interactions but the structure of that web may be critically modified by the web of spatial interactions among the species.

Empirical studies of habitat fragmentation and multitrophic interactions

There have been very few if any studies in which the classical metapopulation processes have been shown clearly to mediate the regional coexistence of interacting species (the most convincing example is Holyoak and Lawler, 1996; for a review see Harrison and Taylor, 1997). This is likely because few studies of multitrophic level interactions are conducted at a large spatial scale over many generations, and because a great deal has to be understood about the habitat and the biology of each species in order to draw conclusions about the relative contributions of large-scale and small-scale factors to the stability of populations of interacting species. In spite of the complexity inherent in simultaneously addressing individual (local) interaction, space, and time, a handful of empirical studies of multitrophic interactions have explicitly considered the large-scale spatial distribution of interacting species (Hopper, 1984; Kareiva, 1987; Roland, 1993; Walde, 1995b; Holyoak and Lawler, 1996; Roland and Taylor, 1997; Tscharntke *et al.*, 1998; Lei and Camara, 1999; Komonen *et al.*, 2000; Kruess and Tscharntke, 2000). These studies compare the potentially

critical role of spatial scale, habitat fragmentation, and species' dispersal behavior among species at different trophic levels, or among different species at the same trophic levels.

Several recent studies compare the relative impact of habitat fragmentation for herbivorous insects (or other lower trophic levels) and their natural enemies (Roland and Taylor, 1995; Jones et al., 1996; Lei and Hanski, 1997; Roland, 1998; Tscharntke et al., 1998; Komonen et al., 2000; Kruess and Tscharntke, 2000; case study, this chapter). These studies primarily show, in agreement with theoretical expectation (Holt, 1997), that species at higher trophic levels suffer more than species at lower trophic levels from a decrease in habitat patch size and an increase in patch isolation, the two primary consequences of habitat fragmentation. This is not surprising because in a dynamic system species at each trophic level can only occur in a subset of the locations in which their host is found, so a fragmented habitat is ever more fragmented at higher trophic levels.

The effect of fragmentation naturally depends on the spatial scale relative to the migration range of each species. Entire insect communities associated with unpredictable host plants may be well adapted to fragmented landscapes. Dubbert et al. (1998) studied the effect of habitat patch size, host plant density, and isolation from occupied habitat patches on the colonization of the grass *Calamagrostis epigeios* by a community of stem-boring herbivores and their parasitoids. The researchers mowed patches of suitable habitat at several distances from source populations to eliminate the insects, and the regrowth of the grass led to very different shoot densities. After one year there was no effect of isolation or area on colonization, rather the presence of herbivores in a habitat patch was best predicted by local host plant density. Dubbert et al. (1998) conclude that the herbivores are adapted to habitat patchiness at the scale of their study (the most isolated habitat patches were 150 m from the source populations), because of the great intrinsic unpredictability in the occurrence of the grass. On the other hand, parasitoids were more likely to colonize less isolated patches, and hence may be considered as less well adapted to the ephemeral occurrence of their host than are the herbivores. It is also important to remember that a parasitoid cannot successfully colonize a habitat patch until a host population has been established, hence it is potentially misleading to compare the dispersal abilities of a parasitoid and a host over a short time interval.

The other focus of recent studies has been on the comparison of the effect of habitat fragmentation on different species at the same trophic

level (such as Jones et al., 1996; Roland and Taylor, 1997; Roland, 1998; case study, this chapter). Roland and Taylor (1997) compared the impact of aspen forest fragmentation on the rate of parasitism by four parasitoids of the forest tent caterpillar (*Malacosoma disstria*). Forest structure (level of fragmentation), host population size, and the rate of parasitism by each parasitoid was measured at 127 points within a $0.8 \times 0.8 \, km^2$ area. The rate of parasitism by three larger species of parasitoid increased with host density and decreased with the degree of fragmentation. Interestingly, the larger-bodied parasitoid species were influenced by fragmentation at the larger spatial scale. The rate of parasitism by the smallest parasitoid increased with decreasing host density and increasing fragmentation. Roland and Taylor (1997) suggest that dense forest probably acts as a dispersal barrier for the small parasitoid but not for the larger parasitoids.

Not surprisingly studies of trophic interactions which include habitat fragmentation generally focus on dispersal behavior. Attributes of species other than dispersal behavior do contribute to their persistence in fragmented landscapes, though for the most part these other attributes are important because they are related to dispersal. For example, within a community of interacting species generalists may be less influenced by habitat fragmentation than specialists if the former are able to use host species living in alternative habitats, reducing the requirement for dispersal to survive (for brief reviews see Harrison and Taylor, 1997; Holt, 1997; for examples see Schoener and Spiller, 1987a, b; Walde, 1994; case study, this chapter). Species with high growth rate or short generation times have more opportunity for dispersal than species that produce few offspring. Species that can reproduce parthenogenetically or are adapted to inbreeding may be less penalized by habitat fragmentation than species lacking these attributes (Godfray, 1994; Hedrick and Gilpin, 1997; Saccheri et al., 1998; Fauvergue et al., 1999; West and Rivero, 2000). The size of a habitat patch can influence many aspects of individual behavior, such as territoriality, with consequences to the response of the species to fragmentation. In a fragmented landscape, habitat patches also differ in ways other than their size and connectivity. These other measures of landscape structure, such as landscape type and complexity, have been shown to influence the relative success of herbivores and their natural enemies, in part through their influence on local interactions (Marino and Landis, 1996; Polis et al., 1998; Tscharntke et al., 1998; Ohsaki and Sato, 1999).

The Glanville fritillary butterfly case study

To illustrate the role of space, habitat fragmentation, and metapopulation dynamics in multitrophic interactions we use results from an extensive research project on the Glanville fritillary butterfly (*Melitaea cinxia*) and its food plants, parasitoids, and hyperparasitoids conducted in the Åland Islands in southwest Finland (Fig. 6.1; for a review see Hanski, 1999). This system is appropriate for the present purpose as it is relatively simple, consisting of just a few species with well-studied local interactions; and because the spatial scale is large (50×70 km) and much is known about the spatial dynamics of the species over several years.

Natural history

The Glanville fritillary butterfly uses two host plant species in the Åland Islands, *Plantago lanceolata* (L.) (Plantaginaceae) and *Veronica spicata* (L.) (Scrophulariaceae) (Kuussaari *et al.*, 1995). The plants are patchily distributed over the 50×70 km area in which the butterfly is found. *Plantago lanceolata* is common in open areas throughout the Åland Islands, but is suitable as a host to the butterfly only in open dry meadows. *Veronica spicata* is found primarily in the western third of the region, almost exclusively in the dry rocky habitats appropriate for the butterfly. Both plants are perennial and reproduce both vegetatively and from seed (Muenscher, 1955), though *P. lanceolata* grows more often from seed than *V. spicata* (Rusch and van der Maarel, 1992).

Local populations of the butterfly occur in dry meadows where the host plants frequently suffer from summer drought (Rosén, 1995; Kuussaari, 1998) and in many cases from successional replacement by other plant species (see Rusch, 1988 for Öland, a somewhat comparable island in the Baltic). Larvae can completely defoliate plants, and in some dense butterfly populations the leaves of all the suitable plants are consumed as the gregarious larvae move from plant to plant in the spring (Hanski and Kuussaari, 1995; S. van Nouhuys, personal observation). However, both *P. lanceolata* and *V. spicata* are perennial and regenerate well during the same season and in the following year. Individual plants are not often killed by *M. cinxia* larvae, but defoliated plants may produce few or no seeds, and their stored resources are probably depleted, hence it is quite possible that in the course of time herbivory by *M. cinxia* may influence the local abundances of their hosts. There is a spatially and temporally dynamic interaction between the herbivore and its food plants at all
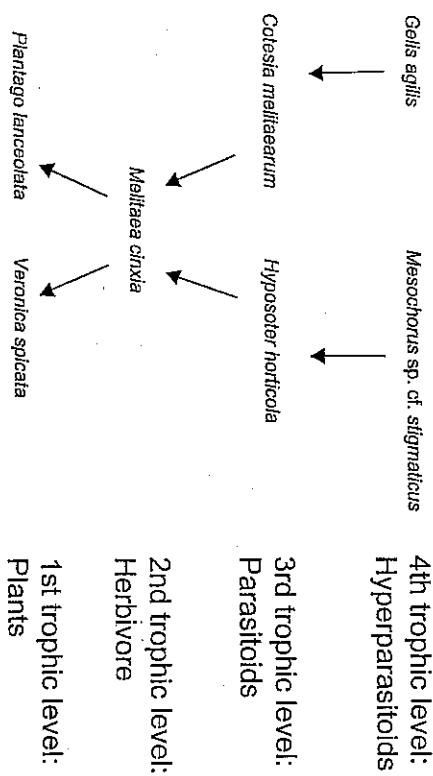
spatial scales, from individual plants to the entire Åland Islands, influenced by the distribution of the two host plant species, spatial variation in genetically based oviposition preference of female butterflies, erratic variation in plant suitability for larval development, and the influence of weather (Hanski, 1999; Kuussaari *et al.*, 2000; I. Hanski and M. Singer, unpublished data; S. van Nouhuys *et al.*, unpublished data).

Each fall the entire study region is surveyed for *M. cinxia* populations. There are some 4000 habitat patches in the study area, of which 300 to 500 are occupied by the butterfly in each year (Kuussaari *et al.*, 1995; Hanski, 1999). Local populations are small, usually made up of a few groups of gregarious larvae, but ranging from one to more than 100 larval groups. Local populations within a cluster of habitat patches (patch networks) comprise classic metapopulations with a high rate of population turnover (Hanski *et al.*, 1995; Hanski, 1997, 1999).

Melitaea cinxia mostly mate once in their natal habitat patch, but substantial migration also occurs, typically to habitat patches within 1 km from the natal patch and especially from small populations in poorquality habitat (Hanski *et al.*, 1994; Kuussaari *et al.*, 1996; Hanski, 1999). Females lay eggs in clusters of 100 to 200 on the underside of host plant leaves in late June. The larvae hatch and live gregariously in silken nests until their last instar late in the following spring, when they disperse to pupate in the litter. The larval development is interrupted by a sevenmonth winter diapause. The larvae and their web are visually conspicuous. The host plants contain high concentrations of iridoid glycosides,

Fig. 6.1. Schematic diagram of the species at each trophic level.

Gelis agilis		4th trophic level: Hyperparasitoids
Mesochorus sp. cf. stigmaticus		
Cotesia melitaearum	Hyposoter horticola	3rd trophic level: Parasitoids
	Melitaea cinxia	2nd trophic level: Herbivore
Plantago lanceolata	Veronica spicata	1st trophic level: Plants

which the larvae sequester (M. Camara, unpublished data) probably as protection against generalist predators (Bowers, 1980, 1983; Camara, 1997).

There are two primary larval parasitoids of M. cinxia in the Åland Islands, Cotesia melitaearum (Wilkinson) (Braconidae:Microgastrinae) and Hyposoter horticola (Gravenhorst) (Ichneumonidae: Campopleginae) (Lei et al., 1997). These wasps compete for hosts (Lei and Hanski 1998, van Nouhuys and Tay, 2001), and they kill a significant fraction of the butterfly larvae (Lei et al., 1997; Lei and Hanski, 1998). The two parasitoids differ greatly in their morphology, phenology, behaviour and distribution (Lei et al., 1997; Lei and Hanski, 1998; S. van Nouhuys, unpublished data). We use these two parasitoids, both of which are involved in a strong interaction with the host and their specific hyperparasitoids, to compare the role of space and habitat fragmentation for species at the same trophic level, but with dissimilar multitrophic interactions, spatial population structures, and population dynamics (Table 6.1).

Each primary parasitoid has an important secondary parasitoid or hyperparasitoid (Fig. 6.1). Hyposoter horticola is parasitized by the mobile solitary larval hyperparasitoid Mesochorus sp. cf. stigmaticus (Brischke) (Ichneumonidae: Mesochorinae). In contrast, Cotesia melitaearum is commonly parasitized by several solitary wingless generalist cocoon parasitoids in the genus Gelis, primarily Gelis agilis (Fabricius) (Ichneumonidae: Cryptinae) (Table 6.1). While using C. melitaearum cocoons Gelis are strictly speaking pseudohyperparasitoids, because they lay eggs on the immature parasitoids after they have left the host and made a cocoon (we nonetheless refer to them as hyperparasitoids). In addition to the two primary parasitoids and their two hyperparasitoids, there are four generalist pupal parasitoids of M. cinxia about which little is known apart from their names (Lei et al., 1997).

Multitrophic interactions between the plants, the herbivore, and the primary parasitoids

Spatial variation of host plant qualities

Plantago lanceolata and V. spicata synthesize and maintain high concentrations of iridoid glycosides which probably deter generalist herbivores and their predators (Bowers, 1991; Stamp, 1992; Stamp and Bowers, 1996; Camara, 1997), but may attract specialists (Bowers, 1983; Oyeyele and Zalucki, 1990) such as M. cinxia and its specialist parasitoids. In the Åland Islands the concentrations of aucubin and catalpol, the two main iridoid

Table 6.1.

Species	Generations	Specificity	Dispersal behavior	Regional distribution	Metapopulation structure[a]
Hyperparasitoids					
G. agilis	Several per year	Generalist	Walk, aggregate	Ubiquitous	No
M. stigmaticus	One per year	Specialist?	Strong flier	Wide	No?
Parasitoids					
C. melitaearum	Three per year	Specialist	Weak flier	Narrow	Yes
H. horticola	One per year	Specialist	Strong flier	Wide	No
Herbivore					
M. cinxia	One per year	Specialist	Intermediate flier	Wide	Yes
Plants					
P. lanceolata	Perennial	Widespread	Seed	Wide	No
V. spicata	Perennial	More restricted	Seed	Intermediate	Yes?

Notes:
[a] "Metapopulation structure" means that the spatial occurrence of the species is strongly influenced by the connectivity of habitat patches.

glycosides, vary greatly between plant individuals, and are on average higher in P. lanceolata than in V. spicata (M. Nieminen and J. Suomi, unpublished data). This variation may contribute to the observed spatial variation in host plant use by the butterfly. Preliminary results indicate that the concentration of aucubin is higher in those P. lanceolata individuals on which females have oviposited in comparison with plants on which females have not oviposited (M. Nieminen and J. Suomi, unpublished data).

The non-volatile iridoid glycosides produced by P. lanceolata and V. spicata are sequestered by M. cinxia larvae (M. Camara, unpublished data). Generally, insect larvae that have sequestered iridoid glycosides are unattractive to some predators and parasitoids but attractive to others (Montllor et al., 1991; Stamp, 1992; Theodoratus and Bowers, 1999). Cotesia melitaearum females spend a significant amount of time, occasionally even days, attending the web of a particular M. cinxia larval group. During this time they touch larvae and groom frequently, but rarely parasitize (Lei and Camara, 1999). Wasps possibly evaluate larvae based on the iridoid glycoside concentration in the larval cuticle, though we do not know whether they would select larvae with high or low levels of iridoid glycosides. While defensive chemicals produced by plants and sequestered by specialist herbivores are likely to be attractive to specialist parasitoids, high levels of compounds such as iridoid glycosides can be detrimental to immature parasitoid development (Campbell and Duffy 1979; Gauld and Gaston, 1994; Reitz and Trumble, 1996).

Volatile compounds produced by host plants and herbivore-infested host plants are widely known to be attractive to parasitoid wasps (Vet and Dicke, 1992; Turlings et al., 1995, chapter 7, this volume). Plantago lanceolata and V. spicata produce volatile compounds (Fons et al., 1998), but the behavioral response by herbivores and their natural enemies to these chemicals has not been studied. The role of host plant in the parasitism of herbivores is of course not limited to chemical signals. First, the nutritional quality or toxicity of a host plant may affect the physiological resistance of the herbivore to parasitism, or the length of time it is available to parasitism. Second, the vulnerability of parasitoids to competitors and their own natural enemies may differ between food plant species. Cotesia melitaearum compete with H. horticola for host larvae, and in the early spring cocoons are subject to extremely high predation and hyperparasitism (Lei and Hanski, 1997, 1998; van Nouhuys and Tay, 2001). If mortality of parasitoids due to competition and natural enemies were to differ between the host plants, or between the habitat patches in which the

plants are found, the rate of successful parasitism on the two host plants would also differ. Finally, the small-scale spatial distribution of host plants is likely to affect parasitoid searching efficiency. Veronica spicata has a more clumped small-scale occurrence than P. lanceolata, which leads to aggregation of host larval groups. If the searching ability of C. melitaearum is higher when hosts are aggregated, which seems likely, then larval groups on V. spicata would suffer more parasitism than those on P. lanceolata (van Nouhuys and Hanski, 1999).

Landscape structure and interactions with the parasitoid Cotesia melitaearum

Cotesia melitaearum is a small and rather sedentary species that has two to three generations per year and gregarious larvae (several parasitoid larvae per host individual). Cotesia melitaearum is relatively rare both in terms of population sizes and the number of local populations (Lei and Hanski, 1997; van Nouhuys and Tay, 2001). Each spring all known M. cinxia populations have been surveyed for C. melitaearum cocoons, but this survey remains necessarily somewhat superficial. To obtain a more accurate picture of the occurrence of the parasitoid, each M. cinxia population in all patch networks that had ever been occupied by C. melitaearum since 1993 was searched thoroughly in 1997–2000 and in some parts of the study area also in the previous years (Fig. 6.2). In this material, the fraction of M. cinxia populations occupied by C. melitaearum ranged from 9% to 20% and many populations persisted only for a couple of years.

Large well-connected populations of both the butterfly and the parasitoid C. melitaearum persist longer than isolated small populations, and population persistence of the parasitoid is associated with large host population size (Hanski, 1999). Within a habitat patch, the oviposition behavior and between-plant movements of both the host butterfly and parasitoids are affected by local host plant distribution. Host plant species affect the butterfly metapopulation dynamics because ovipositing female butterflies have host plant preferences, the plants are not similarly distributed, and there is regional genetic variation in host plant preference (Kuussaari et al., 2000). Additionally, the plants do not respond equally to weather conditions. Host plant species affect the metapopulation dynamics of the primary parasitoid C. melitaearum indirectly via the effects on the herbivore population size and distribution, and directly because the parasitoids are more successful where the host larvae feed on V. spicata. Local host populations feeding on V. spicata are more likely to be
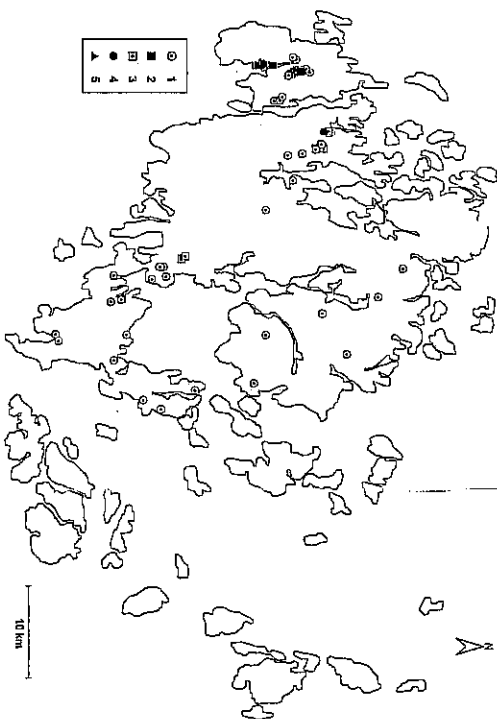
Fig. 6.2. The locations of the known populations of the parasitoid *Cotesia melitaearum* in the Åland Islands from 1997 to 2001. Symbols represent populations that have persisted at least one to five years. Notice that the more permanent parasitoid populations occur in a few clusters. Many of the populations that were observed in only one year are likely to be "remnants" of previously more extensive distributions (the parasitoid has been relatively sparse in recent years).

colonized by the parasitoid, and the parasitoid is less likely to go extinct, than in the case of host populations feeding on *P. lanceolata* (van Nouhuys and Hanski, 1999).

Based on the above-described empirical results, we may infer that if the habitat patches were to become substantially more fragmented, *C. melitaearum* would not be able to persist in the landscape. Similarly, the parasitoid would suffer if the host plant species composition used by the butterfly were to become more *P. lanceolata* dominated. In contrast, if well-connected habitat patches were to become increasingly occupied by the butterfly, or if the host plant use became increasingly *V. spicata* dominated, local populations of *C. melitaearum* would persist longer and would more frequently colonize nearby host populations.

Currently most *C. melitaearum* populations in the Åland Islands are so

small that they are unlikely to have a big effect on host population size or host population dynamics (van Nouhuys and Hanski, 1999; van Nouhuys and Tay, 2001), and most host populations currently not used by the parasitoid are unlikely to be quickly colonized because they are out of the range of dispersal by the parasitoid (S. van Nouhuys and I. Hanski, unpublished data). However, in one network of butterfly populations intensely studied in 1993–1996, *C. melitaearum* apparently caused a large decline of many local host populations. In this case the populations of the host butterfly were tightly clustered and some of the populations were initially exceptionally large [Lei and Hanski, 1997]. Thus, while the parasitoid currently persists at a very low level, not measurably affecting the population dynamics of its host, the parasitoid could become a more important player in the host dynamics if the host availability were to increase, potentially mediated by the distribution of the host food plants.

Landscape structure and interactions with the parasitoid *Hyposoter horticola*

In contrast to *C. melitaearum*, *H. horticola* is a large, solitary, mobile and abundant parasitoid. Several results suggest that isolation of host populations has little or no effect on the ability of *H. horticola* to colonize host populations. Lei and Hanski (1998) found that in a network of 50 tightly clustered habitat patches there was a negative effect of isolation (distance from possible source populations weighted by the sizes of these populations) on colonization by *C. melitaearum*, but isolation did not have any effect on the colonization and occupancy of habitat patches by *H. horticola*. In the spring of 1999, we sampled *M. cinxia* populations for *H. horticola* throughout the Åland Islands to measure the effect of isolation over a larger spatial scale, within the entire 50×70 km study area. We sampled host larvae from 50 populations to cover a range of patch connectivities and population ages. Ten to 60 (mean 26) larvae were sampled from each population, taking haphazardly a few larvae from each larval group. The host population was classified as established "old" ($n=30$) if it had existed for more than two years, and newly colonized "new" ($n=17$) if it had been colonized in the previous summer. We calculated the connectivity of each host population using the measure S (Hanski, 1994),

$$S_i = \sum_{j \neq i} \exp(-\alpha d_{ij}) N_j$$

The level of connectivity of patch i is thus calculated by taking into account the distances between the focal patch i and each of the source patches j (d_{ij}), as well as the sizes of the source populations, estimated as the number of host larval groups (N_j). All $M.$ $cinxia$ populations were considered to be potential source populations because $H.$ $horticola$ is found in the majority of host populations and because the complete distribution of $H.$ $horticola$ was unknown. For parameter α we used the value of 1 km^{-1}, which is our rough estimate of the migration range of the parasitoid. The analysis showed no association between the presence of the parasitoid and the age of the host population nor its level of connectivity. We also analyzed whether there was any association between the fraction of host larvae parasitized and the age of the population using analysis of variance. On average, 18% of the larvae were parasitized per sample, and again we found no association between parasitism and connectivity (Fig. 6.3) nor between parasitism and the age of the host population. These data strongly suggest that $H.$ $horticola$ can be found in isolated and well-connected populations equally often, and that it does not take the parasitoid long to find newly colonized host populations.

The local population sizes of $H.$ $horticola$ are relatively large because 20% to 30% of the larvae in each larval group are parasitized (S. van Nouhuys and I. Hanski, unpublished data). Therefore, $H.$ $horticola$ is present basically everywhere in large numbers and it shows no evidence of having a metapopulation structure in the Åland Islands.

The impact of the first trophic level (host food plant) on $H.$ $horticola$ is much weaker than the impact of the first trophic level on $C.$ $melitaearum$, as $H.$ $horticola$ is not sensitive to plant distribution. Because of its superior dispersal ability, $H.$ $horticola$ would likely persist at about the same level if the network of habitat patches were to become substantially more fragmented. However, below we discuss how competition between the parasitoids and their interaction with the hyperparasitoids makes this conclusion more complicated.

Multitrophic interactions between the herbivore, the parasitoids, and the hyperparasitoids

The two abundant hyperparasitoids have very different roles in multitrophic interactions (Table 6.1). $Gelis$ $agilis$ (and the other less common $Gelis$ species) are flightless generalists that aggregate where $C.$ $melitaearum$

Fraction of sample parasitized (0.0, 0.1, 0.2, 0.3, 0.4, 0.5) vs **Connectivity** (0.0, 0.5, 1.0, 1.5, 2.0, 2.5)
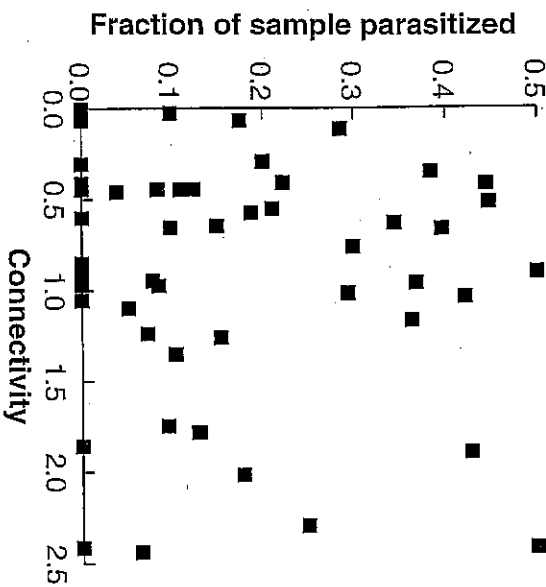
Fig. 6.3. The association between the fraction of $Melitaea$ $cinxia$ larvae parasitized by $Hyposoter$ $horticola$ in a sample and the connectivity of the habitat patch from which the sample was collected. The fraction of larvae parasitized in samples from isolated populations (low value of connectivity) was not significantly different from the fraction of larvae parasitized in samples from well-connected populations.

density is high and can even cause local extinction of $C.$ $melitaearum$ populations, which affects large-scale population dynamics of the host (Lei and Hanski, 1997; van Nouhuys and Hanski, 2000; van Nouhuys and Tay, 2001). Unlike the primary parasitoids, $G.$ $agilis$ females are probably not attracted to particular host plant species and they are extreme generalists, using many families of Hymenoptera as well as Lepidoptera, Coleoptera, and even spider egg cases as hosts (Schwarz and Shaw, 1999). In addition, $C.$ $melitaearum$ cocoons are not found in particularly close association with the host plants of their host insect. The population dynamics of $Gelis$ $agilis$ are likely to be largely disconnected from the dynamics of the primary parasitoid, the butterfly, and the host food plants, even though $G.$ $agilis$ is wingless and disperses on foot.

In contrast to $G.$ $agilis$, the hyperparasitoid $Mesochorus$ sp. cf. $stigmaticus$ probably uses only the host parasitoid $H.$ $horticola$ in the Åland Islands (Lei et al., 1997). $Mesochorus$ $stigmaticus$ is a true solitary hyperparasitoid that lays

eggs into the larvae of H. horticola within the host larva on the host food plant. Mesochorus stigmaticus may respond to the same host plant cues and is subject to the same herbivore defences as H. horticola. Mesochorus stigmaticus is a strong flier, and has been found in most host populations in the Åland Islands where it has been sampled (S. van Nouhuys and I. Hanski, unpublished data). The sample of host caterpillars from 50 butterfly populations used to analyze the dispersal ability of H. horticola (above) also illustrates the dispersal ability of M. stigmaticus. Thirty-seven of the 50 host caterpillar samples contained H. horticola, and of them, 23 contained the hyperparasitoid M. stigmaticus. In these 23 parasitized populations, the mean fraction of H. horticola hyperparasitized by M. stigmaticus was 38%. Logistic regression and analysis of variance showed no association between the presence of or the fraction of H. horticola hyperparasitized by M. stigmaticus and the level of population connectivity nor the age of the butterfly host population. The sample sizes are small, but these data suggest that M. stigmaticus is not limited by dispersal ability in the Åland Islands.

At the largest spatial scale, among the different islands in the Åland archipelago, isolation makes a difference. Thus the large island of Kumlinge (c. 100 km² east of the main Åland Islands (c. 30 km isolation, mostly by sea) has a relatively small metapopulation of Melitaea cinxia, with some tens of small populations in the past eight years. Of the parasitoids, only H. horticola occurs on this island, whereas C. melitaearum and the hyperparasitoid Mesochorus stigmaticus are absent (M. Nieminen, personal communication).

Because H. horticola parasitizes a large but relatively constant fraction of Melitaea cinxia larvae, its main effect on M. cinxia is to make the local population sizes smaller and more prone to extinction than in the absence of the parasitoid. On the other hand, if H. horticola were absent, the butterfly populations would be more vulnerable to parasitism by C. melitaearum. The hyperparasitoid Mesochorus stigmaticus appears to reduce the numbers of H. horticola relatively uniformly over the whole region in the same way as H. horticola reduces the population size of the herbivore.

Competition between the primary parasitoids

In order for two parasitoids to share a single host species there must be mechanisms for partitioning the resource or some other specific mechanism of coexistence. Hyposoter horticola disperses among host populations much more readily than C. melitaearum, and hence the majority of H. horticola are in host populations unoccupied by C. melitaearum. In contrast,

both primary parasitoids are present in the 10%–20% of the butterfly populations occupied by C. melitaearum. Because C. melitaearum populations are most persistent in well-connected large host populations, and especially where V. spicata is the dominant host plant species, it is mostly under these conditions that direct competition between the two primary parasitoids of Melitaea cinxia is likely to occur.

Lei and Hanski (1998) showed that C. melitaearum is a superior competitor within host populations. They found that when both parasitoids were present in a local population, the fraction of larvae parasitized by H. horticola in a larval group also occupied by C. melitaearum was low, 18% on average, whereas when H. horticola was the only parasitoid in a larval group, the mean fraction of larvae parasitized was 33%. In addition, within a habitat patch the larval groups parasitized by C. melitaearum are less isolated from each other than the larval groups without C. melitaearum. On the other hand, the competitive interaction between the two parasitoids is complex because there are three generations of C. melitaearum during each generation of H. horticola. Consequently, immature parasitoids may meet within host larvae under three different competitive conditions. In a laboratory experiment van Nouhuys and Tay (2001) found that when the third generation of C. melitaearum parasitize host larvae already occupied by H. horticola, the latter suppress the development of C. melitaearum larvae. Therefore, though C. melitaearum has proven to be the superior competitor at the population level [Lei and Hanski, 1998), it is the inferior competitor in one of its three generations during each H. horticola (and host) generation.

Conclusions

In the introduction, we posed the questions to what extent local multitrophic interactions in a fragmented landscape are influenced by regional spatial processes, and to what extent the large-scale spatial processes are influenced by the outcome of local interactions. In a metacommunity with high turnover of local populations, as exemplified by the M. cinxia metapopulations and the associated host plants, parasitoids, and hyperparasitoids, the answer to the first question is conclusively affirmative. Not all species are present in every habitat patch, and the interactions among the species that are present are greatly affected by the absence of the remaining species. This is most obvious in the case of the host plant that is not regionally preferred by the ovipositing butterflies (heavily

used only if the preferred host plant is absent), and in the case of the competing primary parasitoids.

The answer to the second question—whether local processes influence regional dynamics—is less obvious but also affirmative. There is evidence showing that the "match" between the oviposition preference of migrating butterflies and the host plant composition in the empty habitat patch influences the rate of successful establishment of new populations (I. Hanski and M. Singer, unpublished data), and we have shown how the extinction and colonization rate of the primary parasitoid *C. melitaearum* is influenced by the food plant species of the host insect population (van Nouhuys and Hanski, 1999). It is thus clear that a comprehensive understanding of multitrophic interactions in fragmented landscapes remains incomplete unless the spatial dimension is explicitly considered.

Turning to the theoretical predictions about multitrophic interactions in space, it is evident that the length of the food chain is limited by metapopulation dynamics. We observed that on the island of Kumlinge with a relatively small butterfly metapopulation consisting of some tens of small local populations, of the parasitoids only *H. horticola* is present, whereas its competitor, *C. melitaearum*, and its hyperparasitoid, *Mesochorus stigmaticus*, are absent. This pattern is consistent with the theoretical expectations because *H. horticola* is the better disperser of the two primary parasitoids, and the fourth trophic level (the hyperparasitoid *M. stigmaticus*) is expected to drop out first from the metacommunity in a small patch network. It may also be significant that of the host plant species only *P. lanceolata* occurs in Kumlinge, on which the parasitoid *C. melitaearum* does less well than on *V. spicata*.

A recent study by Komonen et al. (2000) has strikingly illustrated how habitat fragmentation is likely to truncate food chains in a different ecological setting. Komonen et al. (2000) studied the insect community inhabiting the bracket fungus *Fomitopsis rosea* in continuous and fragmented old-growth forests in Finland. The numerically dominant food chain consisted of the fungus, the tineid moth *Agnathosia mendicella*, and the tachinid parasitoid *Elfia cingulata*. The median number of trophic levels decreased from three in areas of continuous old-growth to one in 10-ha fragments of old-growth that had been isolated for longer than 12–32 years. Such truncation of food chains as a consequence of habitat fragmentation is probably a common occurrence, because species in many metacommunities are not adapted to fragmented or unstable habitats. The mechanisms that lead to the shortening of food chains in newly

fragmented habitats involve spatial processes, especially processes limiting dispersal and colonization, but also the traditional multitrophic level interactions.

Acknowledgments

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